

Relationship between regional climate change and primary ecosystem characteristics in a lagoon undergoing anthropogenic eutrophication, Lake Mokoto, Japan



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ABSTRACT

Annual-scale environmental and ecosystem changes since the mid-19th century were reconstructed in a seasonally frozen lagoon, Lake Mokoto, located along the Okhotsk Sea coast of Hokkaido, northern Japan. X-ray fluorescence (XRF) and diatom analyses of laminated sediment were conducted to determine the impact of short-term climate oscillations and anthropogenic eutrophication on the lagoon ecosystem. In this lagoon, eutrophication has progressed since the early 20th century due to deforestation and human activity in the catchment area, such as development of the cattle industry and field agriculture. In particular, the sedimentation rate of Lake Mokoto and potassium and phosphorus contents of lake sediment have increased rapidly since 1970, in association with an increase in the number of cattle. In addition, the Lake Mokoto ecosystem shows inter-annual and decadal cyclic fluctuations that are separate from the anthropogenic effects. Prior to anthropogenic eutrophication, the nutrient condition of Lake Mokoto showed a close relationship with the Pacific decadal oscillation (PDO). The growth of seagrass, inferred from epiphytic diatom abundance, showed a clear decadal cycle following variation in solar irradiance.

1. Introduction

Coastal lagoons generally exchange a portion of their water with the ocean, regularly or intermittently, through a restricted inlet in the sand barrier. Coastal lagoon conditions can be influenced by freshwater and sediment inflow from the catchment's river. Thus, coastal lagoons have a complex ecosystem affected by various climatic and environmental factors, such as precipitation, sea level, and wind direction (Viaroli et al., 2007; Lillebø et al., 2015). Furthermore, coastal lagoons occur in lowland plains, which are also sites of human and economic activity. High organic loads from aquaculture facilities or factories in the catchment area are often problematic, causing water quality deterioration (Pillay, 2004). It often happens for a lagoon that the introduction of new aquaculture sites, the building of a factory and developments in farming activities in the catchment have adverse impacts on the natural biodiversity and the traditional fishery systems which have been contributed to the livelihoods of the surrounding fishing communities (Kennish and Paerl, 2010). To maintain the ecosystem and

support sustainable use of lagoons for fisheries and tourist resources, it is necessary to understand the lagoon ecosystem and its controlling factors. The best way to clarify the relationships among lagoon water quality, ecosystem health, and numerous related environmental factors is to conduct long-term monitoring. However, a great deal of labour and time are needed for such monitoring, and therefore it has been carried out in only a few locations. As an alternative monitoring procedure, sediment core analysis is often performed. Changing water quality and ecosystem health in a lagoon shift the lagoon's chemical, mineral, and plankton characteristics. Therefore, past water quality and ecosystem factors can be reconstructed based on analysis of these components in the lake-bottom sediment (Stoermer and Smol, 1999; Weckström et al., 2017). Lagoonal environments have high potential for providing high sedimentation rates due to high productivity and inflow of terrestrial material, making it possible to analyse these sediments with high temporal resolution (Ariztegui et al., 2010; Katsuki et al., 2016). In addition, annual laminated sediment layers, called varves, are often deposited in lagoon sediments under anoxic conditions. Annual or

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seasonal changes in ecosystem and climate can be reconstructed using these sediment laminae (Koutsodendris et al., 2017). Furthermore, evidences for the 11-year solar cycle, El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) have all been detected using diatom assemblages in annual laminated sediments, for example in Effingham Inlet, northwest America (Patterson et al., 2013). Patterson et al. (2013) demonstrated that annual and summer precipitation changes, amplified by cloud cover and upwelling variation, induced significant changes in primary production, due to shifts in atmospheric pressure patterns. Other papers have suggested that the impacts of PDO on the lake and lagoon primary ecosystem was triggered by variation in seasonal temperature change and timing of lake ice cover on lakes and lagoon in the subarctic region (Winder and Schindler, 2004; Whitfield et al., 2010; Katsuki et al., 2012). These reports suggested that an environmental driver such as PDO may have variable effects on lagoon and lake ecosystem and environments. It is therefore necessary to examine individual lakes and lagoons for a pattern in the impact of short-term climate variation. In this paper we focus on the short-term impact of short-term climate oscillation in lagoon systems.

The research site, Lake Mokoto is the site of a flourishing fishing industry (Fig. 1). However, the catch rate in Lake Mokoto has decreased

slightly over the last 50 years. The previously important species, smelt, has not been harvested since 1995. Because no regular observations of water quality have been carried out in Lake Mokoto, environmental changes in the lake, and their relationships with aquatic life, are not well understood. Therefore, this study analyzed diatom remains and mineral components of laminated Lake Mokoto sediment to elucidate the impacts of human activity and short-term climate oscillations on the lagoon hydro-environment and its ecosystem over the last 150 years.

2. Study area

The research site is a seasonally frozen lagoon, Lake Mokoto, located on the coast of the Okhotsk Sea in northern Japan (Fig. 1). The bottom sediment of Lake Mokoto is composed of black mud with clear laminations. This lagoon connects to the Okhotsk Sea via a short 2-km-long river, through which seawater enters. The water level range of Lake Mokoto by tide is less than 50 cm. Lake Mokoto is small in area, at 1.1 km², and has a catchment 170 times larger, of about 184 km². There is a vast tract of peat modified for dairy pasture and farm fields, and no urban areas within the catchment. The mean depth of Lake Mokoto is 1.7 m. This lagoon has a central basin with a maximum depth of 4.8 m, as of 2017. The surface conditions of Lake Mokoto are strongly

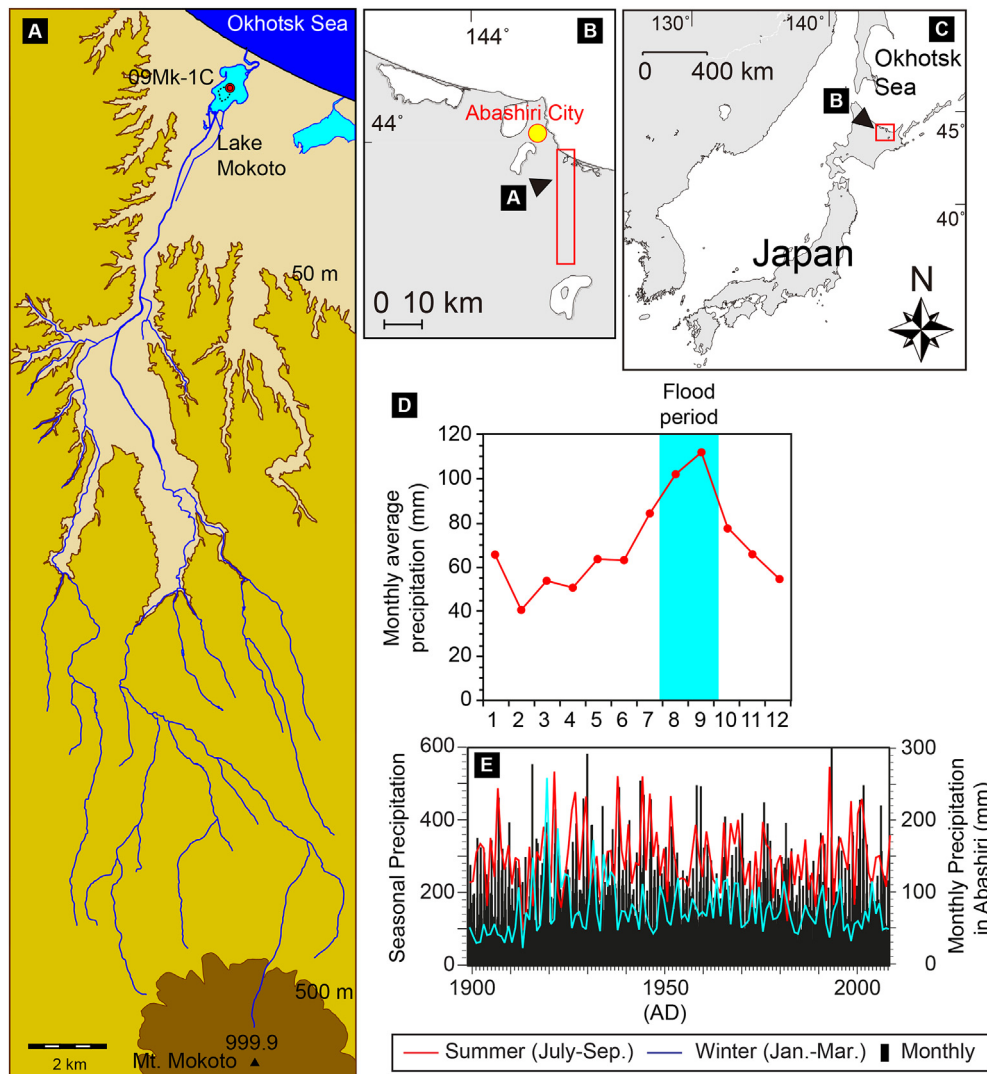


Fig. 1. (A) Schematic map showing the location of Lake Mokoto and its catchment. The 4-m depth isobath in Lake Mokoto is indicated by a dashed line, and the location of piston core sampling is indicated by a circle. Contour lines of 50 m and 500 m are shown. (B, C) Location maps. (D) Monthly average precipitation data between 1980 and 2010 for Abashiri City, which is about 7 km west of Lake Mokoto. (E) Monthly precipitation levels since 1890 at Abashiri City.

influenced by a river inflowing from peatland in the catchment. Therefore, the surface water of Lake Mokoto has high and highly variable nitrogen content (Yasutomi et al., 1995). Surface salinity is also highly variable, ranging from 0 PSU in winter to 20–30 PSU in summer (Hayakawa et al., 2007). A strong halocline is present at a depth of about 1 m. Below the halocline, salinity is almost the same as that of seawater, i.e. 32–33 PSU. The present lagoon is free of anoxic water during winter and spring, although a previous report indicated that the maximum depth of this lagoon was 5.8 m, and water below a depth of 5 m was anoxic in March in 1938 (Hada, 1940).

3. Materials and methods

Core 09Mk-1C, with a length of 178 cm, was obtained from the northern part of the basin of Lake Mokoto (N43°57.448', E144°19.320') using a hand-operated push piston corer (Fig. 1). The sediment core was divided in two immediately after collection at the City Center of Fishery and Science, which is located near the lagoon. The halved core was described in lithological terms. Then, one half of the core was sliced at 1-cm intervals for diatom, ^{137}Cs , and XRF analyses. Intact samples 25 cm long and 5 cm wide were obtained from the other half of the core for soft X-ray imaging.

An age model for this core was constructed based on ^{137}Cs dating and lamina counting (Fig. 2). Lamina sets were counted on soft X-ray images (Fig. 2). Gray scale was analysed for soft X-ray Image by using Image J software. According to a lithological comparison with recent short sediment samples obtained in 2013 and 2015, we confirmed that the high-density layer in Lake Mokoto sediment deposits formed under heavy precipitation. Basically, the high-density layer is deposited in the autumn rainy season (Fig. 1d), and each lamina set in core 09Mk-1C represents 1 year. In fact, thick high-density layers were formed in years of heavy rainfall, exceeding 200 mm in a month. Examples are AD1975, 1992, and 2006 (Figs. 1d and 2). For analysis of the radioactive ^{137}Cs isotope, we used styrene tubes containing about 1–2 g of well-mixed dry sediment, which were analysed using a well-type Ge-detector (EGPC150-P16; Canberra) setup at the Faculty of Education, Shimane University. Measuring anthropogenic “bomb” radionuclides produced during the period of atmospheric nuclear weapons testing is a common method for verifying recently proposed sediment chronologies. The first detection of anthropogenic radionuclides of ^{137}Cs was in 1954, in sediments from the Northern Hemisphere. Maximum ^{137}Cs fallout occurred in 1963, as can almost always be clearly observed in undisturbed sediment records (e.g. Pennington et al., 1973; Klaminder et al., 2012). In this study, 1- to 4-cm sections of samples collected between depths of 76 and 110 cm were analysed to identify the times of first detection and maximum peak bomb ^{137}Cs .

Diatom remnants were analysed throughout the core at 1-cm intervals. Weighed wet samples (about 3–5 mg) were placed in a 100-mL beaker containing hydrogen peroxide (10%, 5 mL) and distilled water (10 mL), and heated on a hot plate for 1 h. Subsequently, a hexametaphosphate surfactant solution was added to the mixture to disaggregate the particles. The samples were mounted on microscope slides using Pleurax mounting medium. Water content was measured to calculate the total number of diatom valves per gram of dry sediment. Observations under a light microscope were conducted at magnification of $1000\text{--}2000\times$. Diatoms were classified with reference to classification schemes used in previous studies (Hendy, 1964; Takano, 1990; Kobayasi et al., 2006; Round et al., 1990; Watanabe, 2005).

For XRF elemental analysis, 66 dry sediment subsamples collected at 3-cm intervals were partially ground using an agate mortar. The powdered sample was dried at 50 °C, and then compressed to make an XRF briquette. Each XRF briquette was analysed using an energy dispersive X-ray fluorescence elemental analyser (MESA-500 W; Horiba Co., Ltd.). The analysis was performed under vacuum conditions using an Rh X-ray tube target with 15- and 50-kV X-ray tube voltages for light and heavy elements, respectively. The analysis time was 250 s for each

X-ray tube voltage (total 500 s). The weight percentages of 11 elements (SiO_2 , Na_2O , MgO , Al_2O_3 , P_2O_5 , S, K_2O , CaO , TiO_2 , MnO , and Fe_2O_3) were quantified using the standard regression method in MESA-500 W. The calibration line for each element was based on a linear equation using 12 standards provided by Dr. H. Fukusawa (detailed in Takata et al., 2014, 2016).

4. Results

4.1. Lithology and age dating

Core 09Mk-1C consists of laminated mud throughout (Fig. 2). The laminae include three layers of differing density: high, middle, and low. The lamination is generally clear throughout the core, but there are some weak laminae at 52–53 cm and 140–150 cm. This core includes 152 lamina sets (Fig. 2). ^{137}Cs activity was detected at depths of 89.5–103.5 cm and 75.5 cm, with maximum activity at a depth of 94.5 cm (Fig. 2). The sedimentation rate increased after the late 1960's, and almost showed a maximum value, $2.02\text{ g cm}^{-2}\text{ year}^{-1}$ in 1991. After that the sedimentation rate gradually decreased (Fig. 3).

4.2. Elemental composition

The most dominant element throughout core 09Mk-1C was Si. The weight percentage of SiO_2 was 50–61 wt% (Fig. 3), and was stable around 58 wt% except near the core top. The Si content was slightly lower since 2002. K_2O and Al_2O_3 show similar tendencies. These constituents gradually increased after 1930, and this trend was pronounced after 1957, particularly in K_2O . Since 1957, K_2O increased from around 0.9 to 1.0 wt%, and Al_2O_3 shifted from 10 to ~12 wt%. P_2O_5 shows a clear change in 1957, hardly appearing before that time and being present at 0.1 wt% ever since. These elemental percentages gradually increased until 1998. The percentage of Fe_2O_3 shifted at 1931, from about 7.5 to 8.7 wt%. On the other hand, the CaO content gradually decreased toward to present during the last 150 years.

4.3. Diatom assemblage

Diatom remains were preserved throughout this core. The total diatom flux and relative abundance of 14 major taxa in core 09Mk-1C are presented in Fig. 4. The total flux of diatoms, including both vegetative valve and spore, varied from 99.3×10^6 to 229.8×10^6 valves $\text{cm}^{-2}\text{ yr}^{-1}$. This total diatom flux has increased since 1980. Fourteen taxa occurred at abundances of more than 5% in several layers: *Cocconeis placentula* (average abundance: 3.1%), *Chaetoceros* spp. resting spores (2.9%), *Cyclotella atomus* var. *gracilis* (2.5%), *Aulacoseira italica* (2.5%), *Melosira lineata* (2.5%), *Cocconeis scutellum* (2.4%), *Skeletonema costatum* (1.9%), *Diatoma mesodon* (1.4%), *Cyclotella atomus* (1.2%), *Thalassiosira nordenskiöldii* (0.9%), *Cyclotella* sp. (0.8%), *Thalassionema nitzschioides* (0.7%), *Cyclotella meneghiniana* (0.5%), and *Thalassiosira pacifica* (0.4%). The abundances of these major taxa were highly variable. A succession of the major taxa occurred between the 1930s and late 1960s. *Cocconeis scutellum* and *D. mesodon* showed high relative abundances before 1930, *Cyclotella atomus* var. *gracilis* before 1950, and *Cocconeis placentula* in the late 1960s. On the other hand, *Chaetoceros* spp. resting spores gradually increased after the late 1960s. *Cyclotella* sp. exhibited spiky peaks in abundance between 1940 and 1970. Constrained cluster analysis and Principal component (PC) analysis were carried out to summarize temporal variations. Cluster analysis was carried out using the PAST program (Hammer et al., 2001). The PC analysis was performed on the 14 major taxa listed above. The contribution to the total variance was low even it was the first PC (PC1) at 18.0%. PC1 consisted of *T. nitzschioides* with a factor score is 0.52, *Chaetoceros* spp. resting spores is 0.46, *T. pacifica* is 0.40 in positive scores, and *C. placentula* is -0.66, *C. atomus* var. *gracilis* is -0.58, *D. mesodon* is -0.57 in negative scores (Table 1).

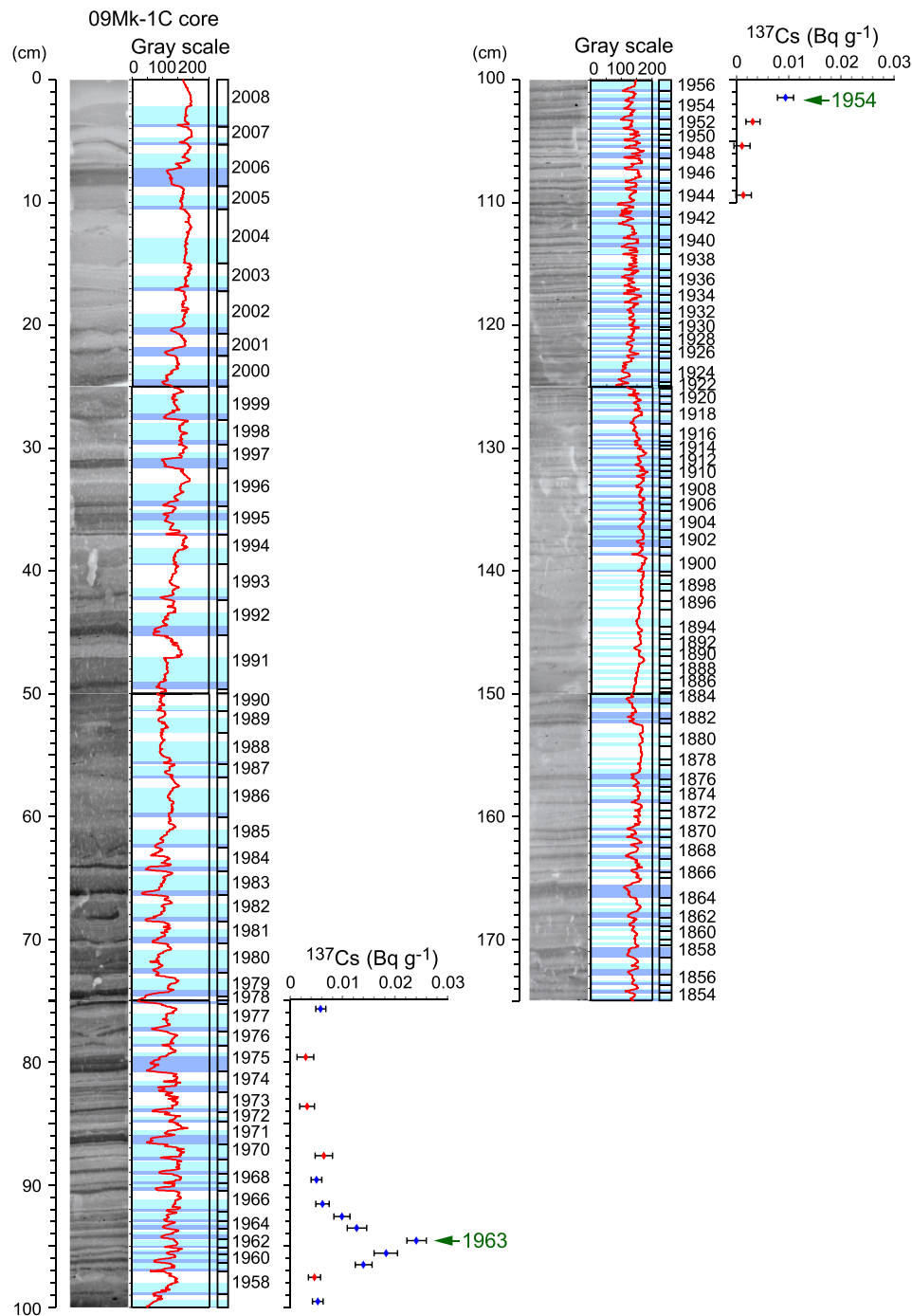


Fig. 2. Lamina lithology based on soft-X ray imaging and down-core ^{137}Cs profiles of core 09Mk-1C.

5. Discussion

5.1. Eutrophication of Lake Mokoto and the Mokoto River

The laminae of 09Mk-1C core rapidly increase in thickness after 1960, and this tendency is particularly noticeable in the middle- and low-density layers (Figs. 2 and 5). The sedimentation rate of this core and the contents of K_2O and P_2O_5 have also rapidly increased since about 1960 (Fig. 3). In particular, the trends of K_2O and P_2O_5 content coincide with the pattern of lamina thickening (Fig. 5). These results imply that Lake Mokoto suddenly became eutrophic after 1960. *Chaetoceros* spp. resting spores started to increase in the late 1960s (Fig. 4). *Chaetoceros* spp., with a large surface-to-volume ratio, is capable of

rapid growth, which is characteristic of systems subject to large nutrient inputs (Su et al., 2004). This increase likely reflects the eutrophication of Lake Mokoto. Total diatom flux increased after the late 1970s (Fig. 4), indicating that the primary productivity of Lake Mokoto increased due to high nutrient supply. What is the cause of this lake eutrophication? After 1970, saprophilous taxa like *C. meneghiniana* appeared in core 09Mk-1C (Fig. 4). On the other hand, freshwater diatoms aside from saprophilous taxa, like *C. placentula*, decreased since the late 1960s. Lake Mokoto is a brackish lagoon. The two opposing trends in these freshwater taxa probably indicates that the water quality of the inflowing Mokoto River changed at that time. This suggests that increasing lamina thickness and K_2O and P_2O_5 fluxes since the late 1960s occurred due to eutrophication of the river. At present, the Mokoto

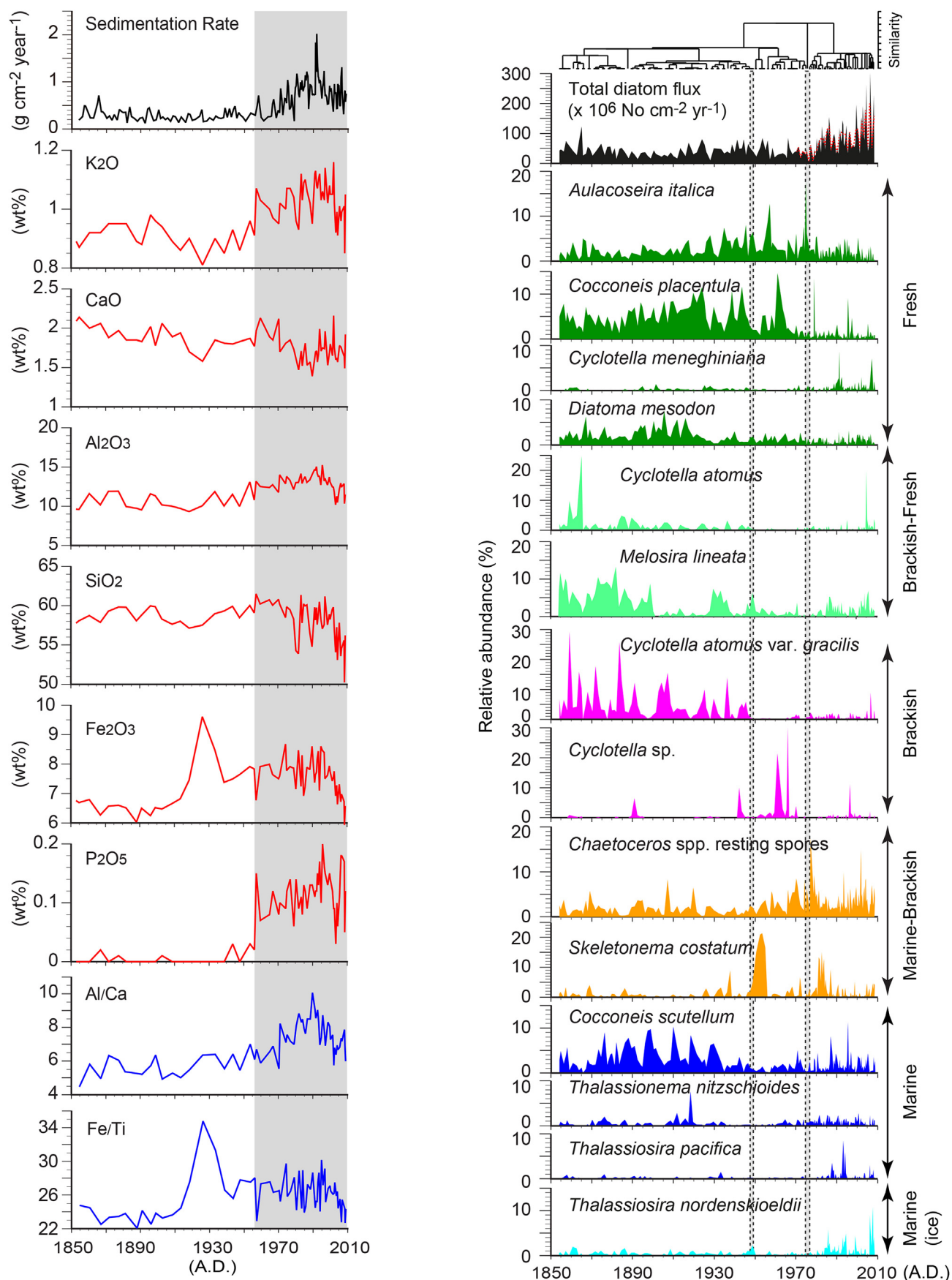


Fig. 3. Temporal variations in sedimentation rate and six mineral components in core 09Mk-1C. Shaded area shows high (> 0.3%) P₂O₅ interval in core - after 1957.

(caption on next page)

Fig. 4. Temporal variations in the total diatom flux and major diatom assemblage in core 09Mk-1C. Red dash line on total diatom flux shows the annual mean flux since 1970. Two shaded areas indicate two major taxonomic transitions determined by Cluster analysis using Horn similarity index. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

List of factor scores for Principal Component 1.

Diatom taxa	PC score
<i>Aulacoseira italica</i>	−0.01
<i>Chaetoceros</i> spp. resting spore	0.46
<i>Cocconeis placentula</i>	−0.66
<i>Cocconeis scutellum</i>	−0.48
<i>Cyclotella atomus</i>	−0.33
<i>Cyclotella atomus</i> var. <i>gracilis</i>	−0.58
<i>Cyclotella meneghiniana</i>	0.38
<i>Cyclotella</i> sp.	0.02
<i>Diatoma mesodon</i>	−0.57
<i>Merosira lineata</i>	−0.38
<i>Skeletonema costatum</i>	0.22
<i>Thalassionema nitzschioides</i>	0.32
<i>Thalassiosira nordenskiöldii</i>	0.52
<i>Thalassiosira pacifica</i>	0.40

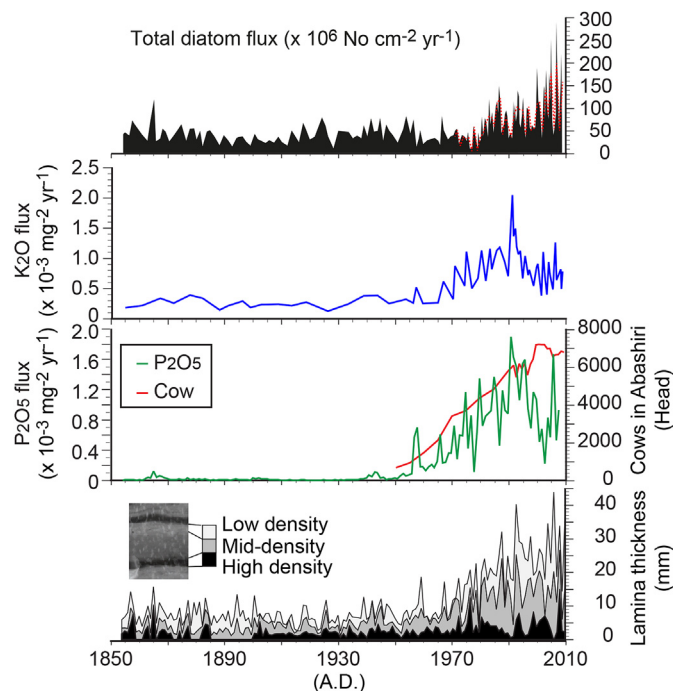


Fig. 5. Temporal variations in total diatom flux, K_2O flux, P_2O_5 flux, numbers of cattle in Abashiri, and lamina thickness in cores 09Mk-1C.

River basin is a productive site of upland crops and dairy farming, and cattle are pastured inside the river levee. Dairy farming began in earnest in Abashiri, including the Mokoto River basin, in the 1950s (Abashiri City Economic Division Agricultural Administration, 2010), and the increase in cattle numbers in Abashiri City follow a trend very similar to the K_2O and P_2O_5 content in the core (Fig. 5). It is thus likely that eutrophication of the Mokoto River and Lake Mokoto was induced by the discharge of cattle faeces into the river.

A shift in the dominant freshwater diatom taxa also occurred around 1930 (Fig. 4). The relative abundance of saproxenous taxa like *D. mesodon* decreased at that time, while the relative abundance of the saprophilous taxon *A. italica* increased. Eutrophication of the Mokoto River probably also occurred around 1930. Between 1900 and 1930,

cultivation of forestland for agricultural use progressed around Abashiri City. Accordingly, forest fires frequently occurred during this period. A huge mountain fire broke out in the Mokoto River basin and burnt about 10,000 ha of forest in May 1930 (Abashiri City Office, 2012). In core 09Mk-1C, the aluminium/calcium ratio (Al/Ca) began to increase in the late 1920s, and the iron/titanium ratio (Fe/Ti) showed a large peak in the late 1920s, followed by persistently high values (Fig. 3). Fe has been widely used to identify variations in terrigenous sediment delivery (Rothwell and Croudace, 2015). Fe contents are often high in lake sediments due to high sediment input accompanying topsoil loss from surrounding agricultural land (Katsuki et al., 2016); thus, Fe/Ti is an indicator of fluvial terrigenous input (Itambi et al., 2010). Al/Ca is also used as an indicator of terrigenous input variability (Nizou et al., 2011). These results indicate that cultivation accompanied by forest fires in the late 1920s caused loss of forests in the Mokoto River catchment basin, which led to inflow of topsoil into the Mokoto River and thus caused the first eutrophication event of Mokoto River and Lake Mokoto. Rapid increase in the sedimentation rate and Al/Ca since the late 1960s indicate that the terrigenous input also increased because of the development of dairy farming.

Cyclotella atomus var. *gracilis* was common in Lake Mokoto before 1950 (Fig. 4). *Cyclotella atomus* var. *gracilis* is a typical diatom of low-salinity, eutrophic lagoons (Kiss et al., 2012). The dominance of *C. atomus* var. *gracilis* indicates that Lake Mokoto was already a eutrophic lagoon before 1930. Subsequently, Lake Mokoto became more eutrophic due to increased inputs of nutrient-rich river water after 1930 and 1970. Since 1950, *C. atomus* var. *gracilis* has rarely appeared. Between 1950 and 1970, another species of small *Cyclotella*, *Cyclotella* sp., showed peaks, but *Cyclotella* sp. is also rarely present after 1970 (Fig. 4). Instead of these small *Cyclotella*, the relative abundance of *Chaetoceros* spp. resting spores increased after 1970. The marine diatom *T. pacifica* and coastal ice-related taxon *T. nordenskiöldii* began to show peaks after 1980. These changes in diatom flora suggest that lagoon salinity increased due to seawater inflow after 1970. In fact, Yasutomi et al. (1995) noted that the anoxic water mass in Lake Mokoto had been reduced due to recent seawater inflow. The sparse laminae of the late 1980s in core 09Mk-1C (Fig. 2) support an increase in the seawater exchange rate at that time. In addition to changes in the aquatic environment of the Mokoto River, the surface salinity of Lake Mokoto has increased since about 1980 due to increasing seawater exchange.

5.2. Short-term climate oscillations of the ecosystem

Distinct from the diatom assemblage changes in about 1930 and 1970 due to eutrophication caused by human activity, some diatom taxa showed interannual or decadal cyclic peaks (Fig. 4). The peaks were particularly notable before Lake Mokoto was influenced by anthropogenic eutrophication. The pattern of fluctuation among small *Cyclotella*, like *C. atomus* var. *gracilis* and *Cyclotella* sp., coincides well with variation in the PDO, particularly before 1970 (JISAO HP, MacDonald and Case, 2005). The PDO is a long-living ENSO like pattern of Pacific climate variability, which is defined as the leading empirical orthogonal function of monthly anomalies of sea surface temperature in the Pacific poleward of 20°N (Mantua et al., 1997). Cold surface temperature anomalies exist in the western and central North Pacific Ocean during the positive (warm) PDO phase while the warm surface temperature anomalies exist during the negative (cold) phase (Mantua and Hare, 2002). When the PDO index was in a positive phase, the relative abundance of small *Cyclotella* often exhibited peaks of over 3% (Fig. 6). Because the PDO phase has a strong impact on sea surface temperature and air temperature around the North Pacific (Mantua and Hare, 2002), there are many examples supporting changes in the aquatic environment and diatom productivity in lagoon and coastal gulf systems that fluctuate with the PDO (Patterson et al., 2004; Kuwae et al., 2006). As described above, *C. atomus* var. *gracilis* dominates under low-salinity and eutrophic conditions. Large fluctuations in small *Cyclotella* that

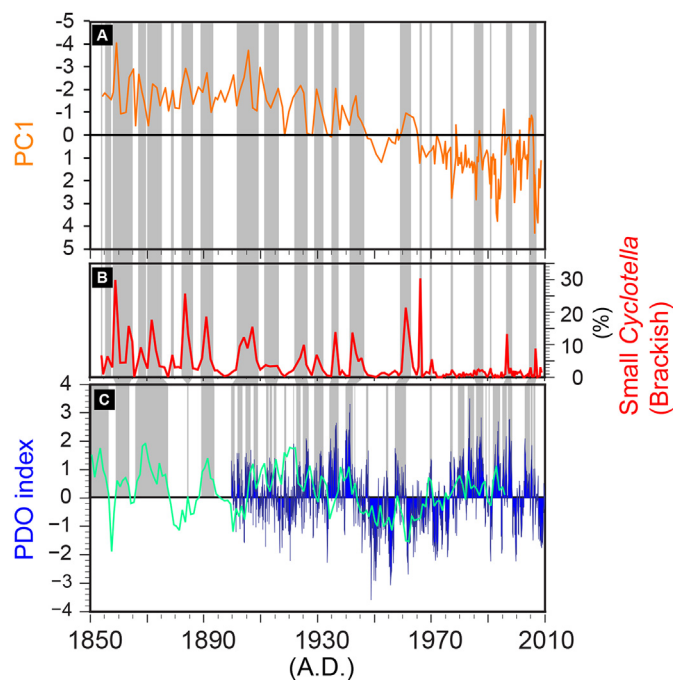


Fig. 6. Temporal variations in A) small *Cyclotella*%, B) the Pacific Decadal Oscillation (PDO) index (JISAO HP: <http://research.jisao.washington.edu/pdo/>) represented by blue area and the reconstructed PDO by tree-ring in the west coast of the North America (MacDonald and Case, 2005) represented by light green line. Grey-scale shadings represent A) over 3%, B) continuous positive phase after AD1900 and positive reconstructed PDO phase before AD1900, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

coincide with the PDO phase suggest that the surface salinity, nutrient conditions, or both, of Lake Mokoto are controlled by the PDO. In core 09 MK-1C, the short-term fluctuation of the PC1 diatom assemblage PC1 also matched PDO phase variation, although the overall trends are rather different (Fig. 6). PC1 probably reflects the surface salinity change, because the taxa have positive scores are marine species and taxa have negative score are belonged to fresh or brackish species, except for exceptional taxon, *C. scutellum* (Table 1). This means that PDO phase has an impact on the lake ecosystem through its influence on salinity in Lake Mokoto. In northeast China, the primary production of lakes follows the PDO phase (Sun et al., 2013), because the weakened land-sea thermal contrast in East Asia during the transition from a negative to a positive PDO phase causes dry conditions in northern China by weakening the East Asian summer monsoon (Qian and Zhou, 2014). Thus, precipitation levels are closely linked to the PDO phase, and primary productivity fluctuates due to variations in terrestrial nutrient inputs.

In the case of Lake Mokoto in Hokkaido, the relative abundances of freshwater diatom taxa do not align with the PDO phase (Figs. 4 and 6). The surface salinity change due to freshwater fluvial inflow tied to rainfall may be weakly related to PDO phase. The environmental conditions and diatom assemblage in a nearby lagoon, Notoro Lagoon, fluctuated in accordance with the PDO phase (Katsuki et al., 2012). Spring temperatures along the Okhotsk Sea coast, including Abashiri City where Notoro Lagoon is located, are highly variable and follow shifts in the PDO index. The timing of lake ice melt depends on these spring temperature changes. As a result, the composition of the spring phytoplankton assemblage and deposition of plankton-origin organic matter in Notoro Lagoon fluctuate widely based on spring temperature and the PDO phase (Katsuki et al., 2012). Lake Mokoto is a seasonally frozen lake, as is Notoro Lagoon. Unfortunately, ice-related diatoms were rare before 1980 in core 09Mk-1C (Fig. 4). It is difficult to

determine the relationship between the PDO phase and historical lake ice conditions based on the diatom assemblage. However, the highest positive score taxon of PC1 is ice-related diatom, *T. nordenskiöldii* (Table 1). It is likely that variations in spring temperature and salinity change, along with lake ice conditions, control the species composition of the spring bloom in Lake Mokoto. In addition to spring temperatures, summer (July–September) temperatures in Hokkaido along the Okhotsk Sea coast, including Kunashir Island, have also coincided well with the PDO phase (Jacoby et al., 2004; Tei et al., 2015). An anoxic water mass exists at the bottom of Lake Mokoto, as indicated by the laminated sediment. An increase in microbial activity with increasing temperature results in O₂ depletion, creating an anoxic bottom water mass due to nutrient elution from the bottom sediment. Therefore, surface nutrient concentrations often change seasonally, generally increasing in the summer months in eutrophic lagoons (Seike et al., 1999; Liikanen et al., 2002). Summer temperature fluctuations corresponding to the PDO phase have likely controlled the surface water nutrient conditions through summer nutrient diffusion in Lake Mokoto, resulting in changes in the relative abundance of *C. atomus* var. *gracilis* that follow the PDO phase.

On the other hand, the relative abundance of *Cocconeis scutellum* has fluctuated on a cycle of 11 years independent of the PDO phase, and this cycle is particularly obvious before 1930 (Fig. 7). *Cocconeis scutellum* is an epiphytic diatom taxon found on seagrass, which particularly favours eelgrass, *Zostera marina* (Jacobs and Noten, 1980; Ohtsuka and Tuji, 1999). *Zostera marina* is a common aquatic plant native to coastal marine environments of the Northern Hemisphere (den Hartog, 1970). This species is also common in lagoons along the Okhotsk Sea coast, including Lake Mokoto. Fluctuations in *C. scutellum* in Core 09Mk-1C likely represent variations in the eelgrass bed area in Lake Mokoto. After 1930, the relative abundance of *C. scutellum* decreased, and its peaks became indistinct (Fig. 7). This change probably occurred because eelgrass beds diminished as Lake Mokoto became eutrophic. It has been reported that the relative abundance of *C. scutellum* in lagoon sediment often decreases to zero after eelgrass beds disappear from the lagoon (Katsuki et al., 2008). Before 1930, the relative abundance of *C. scutellum* aligned well with the solar sunspot cycle, with a phase lag of a few years (Fig. 7). No other planktonic diatom abundance varied periodically with the solar cycle (Fig. 4), meaning that this cycle has a direct effect on eelgrass; it is not due to a shading effect produced by variation in plankton abundance. Variations in solar irradiance during the 11-year sunspot cycle are less than 1 W m^{-2} (Foukal et al., 2006).

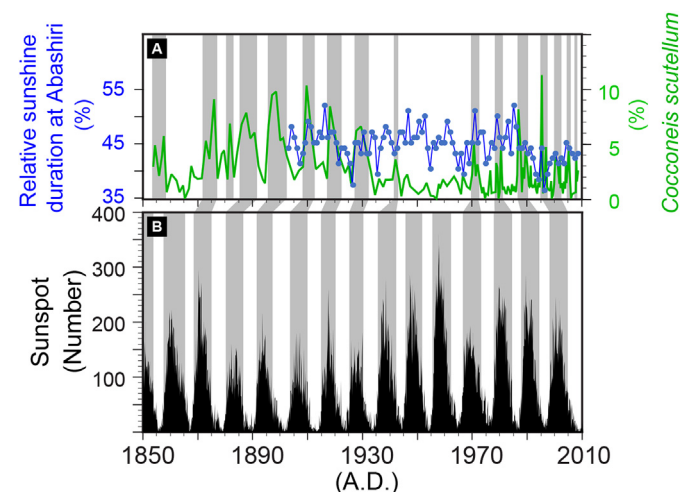


Fig. 7. Temporal variations in A) *Cocconeis scutellum*%, relative sunlight duration at Abashiri City (Japan Meteorological Agency HP: <http://www.jma.go.jp/jma/menu/menureport.html>), and B) sunspot number between 1850 and 2008 (from SILSO: <http://sidc.be/silso/datafiles#total>). Grey-scale shadings represent A) over 3% of *C. scutellum*, and B) over 50 sunspots, respectively.

Light intensity is the primary limit on the distribution of eelgrass beds (Goodman et al., 1995; Hiraokoa et al., 2000), and a small difference in solar irradiance appears to have influenced the distribution of eelgrass beds in Lake Mokoto. On the other hand, relative sunshine duration in Abashiri City also followed a pattern similar to the relative abundance of *C. scutellum* in core 09Mk-1C over the last 100 years (Fig. 6). Although some may doubt that such small variations in solar irradiance could cause a measurable 11-year cycle in eelgrass bed distribution, a stronger case can be made by invoking positive feedbacks related to relative sunlight duration. Moreover, variation in solar irradiance may affect sunlight duration via its impact on cloud cover change over this region. Because solar activity may modify cloud cover via affecting cosmic ray flux which can increase atmospheric ions, leading to enhanced condensation of water vapor and cloud droplet formation (Sun and Bradley, 2002). In any case, our results indicate that the distribution of eelgrass beds in Lake Mokoto has a natural cycle tied to variations in sunlight.

6. Conclusion

Annual-scale high-resolution changes in the lake environment were reconstructed based on analysis of diatom remains and mineral components in the laminated sediment of Lake Mokoto, which is located in northern Japan along the Okhotsk Sea coast. The initial eutrophication step, around 1930 was in a stepwise manner, and this tendency is particularly remarkable since 1970. The initial eutrophication step in about 1930 was caused by expansion of field agriculture and a huge forest fire in the Mokoto River catchment. The next eutrophication step, subsequent to 1970, was induced by increasing cattle numbers in the catchment, and discharge of cattle faeces into the Mokoto River. Aside from anthropogenic eutrophication, the aquatic environment and ecosystem of Lake Mokoto showed interannual and decadal-scale oscillations related to the PDO and the solar irradiance cycle. Due to summer water temperature fluctuations associated with the PDO phase, nutrient concentrations in the surface water follow the PDO phase, causing nutrient elution from the bottom sediment. Furthermore, the distribution of eelgrass beds in Lake Mokoto has followed an 11-year cycle based on sunlight levels.

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